Mechanisms of Speciation

Some species show little geographic variation...

...while others vary quite a bit.
Geographic variation may be gradual...

Geographic Variation in Poisonous Clovers.

... or abrupt.

Terrestrial adults of six species of ambystomatid salamanders.

What is a species?

Because speciation is often a gradual process, it may be difficult to recognize boundaries between species.
For All Species (Spp.) Concepts:

- Spp. consist of groups of “actual” or “potential” interbreeding pop’s.
- Spp. are a fundamental unit of evolution (bridging both macroevolution and microevolution).
- Spp. share a distinguishing characteristic, which is evolutionary independence. This occurs when microevolutionary forces (mutation, selection, migration & drift) operate on each spp. separately.
  - Forms a boundary for the spread of alleles.
  - Different spp. follow independent evolutionary trajectories.

Biological Species Concept (BSC)

- Species are groups of actually or potentially interbreeding individuals that are **reproductively isolated** from other such groups (Mayr).
- Used by the Endangered Species Act (for better or worse).
- What about non-overlapping pop’s, fossil record, & microbes?
Difficulties with the Biological Species Concept

- Asexual reproduction
- Many geographically isolated populations
- Variation in reproductive isolation
- Hybridization and introgression
- Endosymbiont-caused isolation

Asexual reproduction

Many geographically isolated populations
Variation in reproductive isolation

Degree of sexual isolation between populations of *Desmognathus ochrophaeus*

Hybridization and Introgression

Hybrids may form if separated populations rejoin without sufficient genetic differences having accumulated.

Hybridization and Introgression

The movement of a gene from one species into the gene pool of another by backcrossing an interspecific hybrid with one of its parents.
Endosymbiont-caused isolation

**Phylogenetic Species Concept (PSC)**

- The smallest aggregation of populations or lineages diagnosable by a unique combination of character states (Nixon & Wheeler).
- Monophyletic groups derived from a single common ancestor.
- Not standardized, which traits are most important?
Evolutionary Species Concept (ESC)

- A single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies (Simpson).

- Required for fossil record analysis.

- Must be applied carefully and consistently, i.e., “Cryptic species”.

10 Cryptic Species revealed in the neotropical skipper butterfly *Astraptes fulgerator.*

Diagnosing Species in Practice

- Morphology
- Behavior
- Molecular data
What is speciation?

• **Isolation:** Physical separation between pop’s
  • May or may not be required!

• **Divergence:** In habitat use and/or mating tactics
  • Via Selection, Mutation, and/or Drift

• **Completion:** aka Reproductive Isolation
  • 2° Contact via Reinforcement
  • Hybridization events

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Major Questions in Speciation Research

• What is the geographic context of speciation?
• What are the roles that evolutionary forces (selection, drift, gene flow) play in speciation?
• Are few genes or many involved in speciation?
• How long does speciation take?
• Why do some lineages speciate more rapidly than others?
Under the Biological Species Concept, the key to understanding the formation of new species lies in understanding the evolution of reproductive barriers.

Intrinsic vs. extrinsic barriers

(Rem: Mass vs. Weight example)

Prezygotic Barrier: Temporal Isolation

Western Spotted Skunk • breeds in late summer

Eastern Spotted Skunk • breeds in late winter
Prezygotic Barrier: Behavioral Isolation

The posterior lobe of the genital arch in males of three closely related species of Drosophila.

Prezygotic Barrier: Mechanical Isolation

Prezygotic Barrier: Gametic Isolation
Successive stages in each of four models of speciation differing in geographic settings.

- **Allopatric Speciation**
  - Association
  - Geographic isolation disrupts gene flow.

- **Peripatric Speciation**
  - Founder effect
  - Geographic isolation also results in speciation.

- **Sympatric Speciation**
  - No physical separation required.
  - Polyploids especially in plants.
  - Disruptive selection creates divergence in ecological traits.
  - Selection for assortative mating.

- **Parapatric Speciation**
  - Divergence along a gradient.
  - Requires a hybrid zone.
Allopatric Speciation: Vicariance

The Isthmus of Panama formed from 15 Mya to 3 Mya.

Speciation in snapping shrimp across the Isthmus of Panama

7 morphospecies w/o repro
Closest clades show “Final Break” at ~3 Mya
(*) = cryptic species

Allopatric speciation is common in island archipelagoes via Dispersal & Colonization
Successive stages in each of four models of speciation differing in geographic settings.

(C) Parapatric speciation

(D) Sympatric speciation

Range expansion leads to sympatry

Genetic differences result in reproductive isolation

Reproductive Isolation

Byproduct (Mayr) vs. Reinforcement (Dobzhansky)

Reinforcement – type of selection that leads to assortative mating and prezygotic isolation.

Reproductive isolation revisited:

• Both prezygotic and postzygotic barriers increase gradually over time for either model.

• Reinforcement speeds up prezygotic barriers in sympatric sister species through assortative mating.
Pre- or postzygotic reproductive isolation between pairs of populations & species of *Drosophila*

Faster to full isolation, i.e., barrier is complete

**Level of prezygotic isolation between allopatric and sympatric pairs of Drosophila populations**

Faster to full isolation, i.e., barrier is complete

**Sympatric speciation via hybridization**

*Goatsbeards* (*Tragopogon*)
Sympatric speciation via hybridization

Diploid parental species

Tetraploid hybrid species (broader range than parentals)

Diploid parental species

Sunflower speciation

Spokane

Black-bellied Seedcrackers (Pyrenestes)

- Live in marshes in W. Africa
- Eat seeds, primarily of two plant species
- One seed type is small, the other type is large
- Bill dimorphism reflects the effects of disruptive selection

Leads to Assortative Mating and Sympatric Speciation.

Sympatric speciation via ecological niche polymorphism

Linnetic male

Benthic male
Sympatric speciation in the three-spined stickleback

- Probability of speciating
- Limnetic x limnetic
- Limnetic x benthic
- Benthic x benthic

- Same lake
- Different lakes

Hybridization – fitness of hybrids determines hybrid zone and eventual outcome.

- Relative overall fitness
- Plants from basin habitat
- Plants from intermediate habitat
- Plants from mountain habitat

Sagebrush

How many genes are involved in speciation?

- Proportion of males with motile sperm in nonhybrid D. simulans and in backcross hybrids.
- X has a major effect on motility! (i.e., prezygotic barrier)
Sequence divergence of mtDNA between pairs of closely related songbirds

Two meanings of the “rate of speciation” …How long does it take?

• Biological speciation interval
• Time for speciation

• Must grow exponentially
• No extinctions
Estimates of time required for the speciation process in various groups of organisms

Factors promoting rapid speciation

- Many species
- Opportunities for geographic isolation
- Limited mobility
- Short generation time
- Sexual selection
- Ecological specialization

Ecological Specialization